DIFFERENTIATING EVOLUTION FROM ENVIRONMENTALLY INDUCED MODIFICATIONS IN MID-CARBONIFEROUS CONODONTS

by KARL M. CHAUFFE *and* PATRICIA A. NICHOLS

ABSTRACT. Envirotypes are persistent, environmentally induced, potentially inheritable phenotypes that have not been genetically selected for an environment. Unlike ecotypes, envirotypes do not breed true in different environments. The term ecophenotype should be restricted to phenotypic modifications resulting from disease, injury, physical restrictions on growth or to modifications that develop through use. To distinguish evolution from environmentally induced modifications in conodonts one should consider: (1) number of multielement species in the fauna exhibiting modifications; (2) number of elements in the apparatus displaying modifications; (3) uniqueness of modification; (4) occurrence of modified and unmodified forms; and (5) stratigraphical range of modified form. When applied to the conodont fauna from the Carboniferous Barnett Formation in Texas, these criteria suggest that the geniculatan element is not an envirotype or ecophenotype of the ponderosiform element, but that two species of *Idioprioniodus*? are present. Similarly, when applied to the Pa element of the *Taphrognathus varians* apparatus, the criteria suggest that blade position relative to platform and platform ornamentation is not an environmentally induced feature.

PHENOTYPIC modification may result from evolution of the genotype through mutation, hybridization, or alteration of environmental factors. Differentiating evolutionary changes from environmentally induced phenotypic changes is a long-standing problem, especially for palaeontologists. Many terms describe the environment's influence on a phenotype, but we know of no taxonomically neutral term to describe an environmentally induced, persistent, potentially inheritable phenotype for which there is no evidence of genetic selection for an environment. We propose the term envirotype.

Populations with modified phenotypes may represent distinct taxa isolated genetically by evolution, or conspecific ecophenotypes, ecotypes, or envirotypes. For extant organisms, breeding experiments and clines may demonstrate relationships among phenotypes. Recently, comparison of DNA sequences has been used to evaluate the genetic relationship between morphologically distinct populations (e.g. Chesney *et al.* 1993). Fossil populations provide a greater challenge because little genetic material is usually preserved, the organisms are deceased and recognition of clines is more difficult.

Conodont-bearing organisms became extinct in the early Mesozoic. Because the nature of the organism is uncertain, no closely related group has been recognized. Skeletal elements, called conodonts, typically display great variability within isochronous as well as chronologically successive populations. Determining taxonomic relationships among various conodont phenotypes provides a unique and difficult challenge.

Recently, several authors have suggested that some forms of conodont represent ecophenotypes (envirotypes herein) rather than genetically distinct species, subspecies or populations (Merrill 1980; Horowitz and Rexroad 1982; Merrill and Bitter 1984; Merrill and Grayson 1987; Merrill *et al.* 1990; Purnell 1992). This paper proposes criteria for evaluating whether modifications to conodont phenotypes represent evolution or environmentally induced changes. In particular, we shall review the suggestion that the form species *Geniculatus claviger* (Roundy) is an envirotype of the Pb element in the *Idioprioniodus paraclaviger* (Rexroad) apparatus and that the form species

Cloghergnathus globenshii Austin is an envirotype of the Pa element in the *Taphrognathus varians* Branson and Mehl apparatus.

GENOTYPE, PHENOTYPE, ECOPHENOTYPE, ECOTYPE AND ENVIROTYPE

Genotype refers to an organism's genetic constitution, only a part of which may be expressed. Dominant genes mask recessive genes unless the organism is homozygous for the recessive genes. For example, if the genotype is heterozygous for both giantism and dwarfism genes, the organism will have the potential to be large if the giantism gene dominates or small if the dwarfism gene dominates. Should dominant genes not dominate fully, intermediate features may develop. Some characters are controlled by more than one pair of genes. Interaction of the gene complex will determine the potential expression of the characters. Thus, an organism's genotype is generally much more diverse than features and functions indicate.

Although genes define an organism's potential development, a complex interaction between genotype and environment determines the characters and functions ultimately exhibited. The sum of these characters and functions is called the phenotype. Identical genotypes exposed to different environments may produce different phenotypes. Environmental stimuli can repress development of some features and enhance development of others. For example, coiling direction of some foraminiferal tests seems related to water temperature (Bandy 1960). Above a critical temperature, dextral coiling dominates the population; below that temperature the dominant coiling is sinistral. Other organisms alter spine size, and test or valve shape in response to seasonal changes in water viscosity. Incubation temperature determines gender of some reptiles. Body form, sex and size in some insect species are directly related to the food which larvae are fed. Even phenotypically conservative species may show altered growth patterns and markedly different phenotypes under extreme environmental conditions.

Not all characters or functions may display a great diversity of expression. According to Waddington (1957), some characters are 'developmentally canalized'. Development can proceed in only one direction regardless of the environment. These features will display little, if any, variation in different environments. Other features are 'developmentally flexible'. Development can proceed in a variety of ways. These characters may display great differences in diverse environments. For example, to survive, oysters must develop shells (canalized development), but the shape of the shell is controlled by crowding, light intensity and substrate (flexible development).

Intraspecific variation reflects not only genetic diversity but also the diversity of environments inhabited by a species. Each organism's genetic plasticity establishes modes and limits of response to various environmental conditions. If conditions exceed those limits, the organism can no longer respond adequately. Under extreme conditions an organism may not breed or may die. Self-sustaining populations only occur in habitats where environmental conditions are within the range of response for the organisms composing those populations. Phenotype extinction may not result from only genetic extinction, but also from elimination of environments. Similarly, appearance of new phenotypes may result from new genetic variations through mutation (evolution), hybridization or from environmental change.

An environmentally induced, non-inheritable modification of a phenotype has been called an ecophenotype (King and Stansfield 1985; Hale and Margham 1991). We have problems applying this concept as currently used. Implied in the definition is that each species has a standard phenotype which is altered (modified) by abnormal environmental conditions, thereby producing an ecophenotype. As noted above, all phenotypes are, in part, environmentally induced expressions of the genotype. Different environments may produce different phenotypes from the same genotype. Thus, no phenotype can be considered the standard and all phenotypes could be considered ecophenotypes in terms of being environmentally induced. The phenotype considered the standard is usually the most common form, generally reflecting the most widespread environment, or is the form with nomenclatural priority.

A second problem in applying the ecophenotype concept, as currently used, relates to the non-inheritability of phenotypic modifications. As noted by Schmalhausen (1986), organisms only inherit the *potential* to express structure or function. Without proper environmental stimuli no structure or function can be realized. With proper environmental stimuli any modification can be reproduced, if the genetic potential exists within the organism.

Some environmentally modified phenotypes are extremely stable and persist as long as the environment that induces them exists. These stable, persistent phenotypes show a consistency in form to the extent that some have been identified as distinct species, both modern and fossil. If there was not a genetic basis to these environmentally induced modifications, they would vary greatly with each generation. Therefore persistent, consistent, environmentally induced modifications must be considered potentially inheritable and genetically based. We feel it is inappropriate to call these modified phenotypes ecophenotypes.

The term ecophenotype should be restricted to non-persistent, inconsistent, non-inheritable, environmentally induced phenotypic modifications. This would include modifications from disease, injury, physical restrictions on growth or changes that develop through use (e.g. size of musculature and muscle attachment is partially determined by muscle use). These types of modifications are caused by largely random environmental factors and are clearly not inheritable, although the potential response is. As restricted herein, ecophenotype is similar in concept to phenocopy and variant, except in that some variants can be inheritable.

We found no taxonomically neutral term to describe persistent, consistent, environmentally induced, potentially inheritable phenotypes that are not genetically selected for an environment. The term phenotype is not specific and includes all interactions between genotype and environment including ecophenotype and ecotype. Forma, subspecies, ecospecies and ecosubspecies all imply a taxonomic status (Kenneth 1960; Hale and Margham 1991). Variant does not necessarily imply inheritability (King and Stansfield 1985). Ecotype implies that the population has undergone some genetic selection for an environment that differentiates it from other conspecific populations (Kenneth 1960). Raised in a different environment, ecotypes continue to display phenotypic differences from the population native to that environment. The term morph applies to either an individual of a polymorphic population or a variant (King and Stansfield 1985). In the absence of an appropriate term, we propose *envirotype* for persistent, consistent, environmentally induced, potentially inheritable phenotypes that have not been selected genetically for an environment. Unlike ecotypes, different envirotypes raised in the same environment should produce an indistinguishable range of phenotypes.

Most phenotypes, cited in the literature as ecophenotypes, do not conform to our revised definition of this term and are more properly called envirotypes than ecotypes. Chesney *et al.* (1993) demonstrated that fresh water mussels *Margaritifera durrovensis* Phillips and *M. margaritifera* (Linnè) are conspecific. *M. durrovensis* is the phenotype developed in hard water, whereas *M. margaritifera* inhabits soft water. We would call these envirotypes and not ecotypes because no evidence was presented to show significant genetic differentiation. Lack of breeding experiments also requires that ecophenotypes recognized by Chang and Kaesler (1974), Poag (1978), Wang and Lutze (1986), Brazeau and Lasker (1988), Hove and Smith (1990) and Walton and Sloan (1990) be considered envirotypes. Fossil phenotypes cited as ecophenotypes by Owen and Ingham (1988) and Hauser and Grünig (1993) must be considered envirotypes. Breeding experiments and comparison of DNA sequences, required to demonstrate that populations are ecotypes, are not currently possible with most fossils.

DIFFERENTIATING BETWEEN EVOLUTION AND ENVIRONMENTALLY INDUCED CHANGE IN CONODONT MORPHOLOGY

One can determine if extant, modified phenotypes represent distinct taxa or conspecific ecotypes, ecophenotypes or envirotypes through breeding experiments and/or the identification of clines. If a phenotype is raised under a variety of environmental conditions and produces a range of

phenotypes similar to those found in nature living under these environmental conditions, it is obvious that the naturally occurring phenotypes are conspecific. The phenotypes are envirotypes and the various forms do not represent evolutionary change within the species. Using this technique, Schnitker (1974) demonstrated with cloned cultures of *Ammonia beccarii* (Linnè) that *A. parkinsoniana* (Orbigny), *A. advena* (Cushman), *A. beccarii*, *A. catesbyana beccarii tepida* (Cushman), *A. beccarii sobrina* (Shupack), *A. pauciloculata* Phleger and Parker and *A. linnetes* (Todd and Brönnimann) were not true species but only envirotypes (his ecophenotypes).

A cline can demonstrate the close relationship between extreme phenotypes and indicate that end members are conspecific. From a continuous gradation of forms, Poag (1978) concluded that two distinct phenotypes of *Ammonia parkinsoniana* were controlled clinally by variations in temperature and salinity and were not distinct species. Absence of a cline may not be significant. According to Schmalhausen (1986), some modifications attain complete expression at a minimum threshold. Increasing intensity of environmental stimulus does not alter degree of modification. Thus, no cline would be expected. The character either develops fully or is absent.

Comparison of DNA sequences can also be used to demonstrate a relationship between distinct phenotypes. Chesney *et al.* (1993) employed DNA sequences in substantiating that *Margaritifera durrovensis* and *M. margaritifera* are conspecific envirotypes (their ecophenotypes).

Distinguishing between evolution and environmentally induced change is more difficult in fossil populations. Closely related, extant forms should not be used as models in evaluating fossil species. Raup (1972) demonstrated that in some instances the same kinds of differences reflect evolution in one species and environmentally induced change in another.

Clines are also less useful in the fossil record. Lack of spatial and temporal resolution inherent in most palaeontological studies obscures the distinction between isochronous clines and evolutionary sequences. Merrill and Bitter (1984) suggested that morphological changes along a presumed palaeo-ecocline are as likely to represent mixing of end member populations of two closely related species as they are to be ecophenotypes within a species.

Johnson (1981) attempted unsuccessfully to use ontogeny to differentiate 'canalized' and 'flexible' species and thereby identify environmentally induced modifications and evolutionary changes in Jurassic scallops. He proposed that 'developmentally flexible' species should display a decrease in variation with time (ontogeny) in a single environment, but an increase in distinct mean morphologies in different environments. In contrast, he predicted that 'developmentally canalized' species would display few changes.

Conodonts provide a unique challenge in differentiating between evolution and environmentally induced changes. Conodont-bearing organisms have been extinct since the Triassic and the nature of the organism is still uncertain, although many hypotheses have been suggested based upon various unique fossils. No closely related group has been recognized. Although ontogeny is preserved within conodonts, it is not readily accessible because later growth obscures it. Ontogeny is usually interpreted from a size gradation of specimens, despite the problems inherent in this procedure.

We propose the following five criteria to evaluate whether modified conodont phenotypes represent evolution or environmentally induced change (envirotypes). Similar concepts were employed by McKinney and McNamara (1991) in evaluating modified echinoid phenotypes of a species of *Eupatagus*. None of these criteria alone, nor all of them together, can prove that a modified phenotype represents evolution or environmentally induced change. Yet, they do provide a uniform basis for evaluation.

Number of unrelated taxa exhibiting modification

If more than one unrelated conodont apparatus-species in a sample has similarly modified conodonts, the modifications were probably environmentally induced. It is unlikely that two unrelated species evolving in the same environment would evolve similar modifications

simultaneously and independently. The modified phenotypes are most probably envirotypes or ecophenotypes. If the modification is restricted to only one taxon, this may indicate that only the modified taxon was susceptible to the environmental stimulus or that the modification is genetic in origin.

Number of element types exhibiting modification within an apparatus

If only one element type of an apparatus was modified, this may suggest evolution, rather than environmentally induced change. Temperature and salinity have been regarded as the environmental stimuli most probably responsible for inducing alterations in conodont phenotypes. Although physical processes could expose one element type to greater stress because of location within the body, chemical or thermal stress would probably influence all conodont-secreting tissues equally. An analogous example can be seen in mammalian teeth. If exposed during development to insufficient nutrients or an over-abundance of an element, such as fluorine, all teeth develop the same 'abnormalities'. A similar situation occurs in bones. For example, rickets affects the entire skeleton, but is most noticeable in load-bearing bones because of the greater stress.

If several or all conodont types within an apparatus are modified, this probably represents environmentally induced change. Mosaic evolution, as shown in conodonts, suggests that it was unlikely for several conodonts in an apparatus to evolve rapidly and simultaneously, or to evolve the same modification. According to Nicoll (1987), Pa elements evolved the fastest, Pb elements more slowly and the remainder of the apparatus was relatively conservative.

Uniqueness of modification

If the modified phenotype duplicates a common character of conodonts, this may represent an evolutionary trend, parallel evolution, or adaptation to a habitat, rather than an environmentally induced change. If the modification is unique and displays a different microstructure, the modification was probably environmentally induced.

Occurrence of modified forms and unmodified forms

If modified and unmodified phenotypes of an element co-occur throughout their geographical range, the modification is more probably genetic in origin and may represent an evolutionary change. All forms would have been exposed to the same environmental stimuli. If the environment induced a phenotypic change, all forms having the same genotype would display the modification. Modified and unmodified forms co-occurring indicate that genetically distinct groups (subpopulations) existed.

If phenotypes are isolated or display mixing only along the periphery of their geographical ranges, little information is provided to interpret the relationship between the phenotypes. Peripheral mixing of populations could indicate one of three possibilities: they were distinct, environmentally incompatible taxa throughout most of their ranges; at least one phenotype may have been an ecotype (genetically distinct below a subspecies level); or there was post-mortem mixing.

Stratigraphical range of modified forms

Modified phenotypes restricted to a single stratigraphical horizon may represent an envirotype developed in a short-lived environment. This would be further supported if the phenotype is restricted to a specific lithology. Modified phenotypes that persist across many stratigraphical horizons and are associated with a variety of lithologies, are more likely to represent evolutionary

change or an environmentally induced change caused by an environmental factor that left no imprint on deposits.

Modified phenotypes that appear periodically could represent envirotypes which only developed when certain environmental factors were present. The modified phenotype could also have been a distinct taxon which periodically migrated into an area when the environment was suitable. Presence or absence would have been environmentally controlled, but the phenotype was not environmentally induced.

IS *GENICULATUS CLAVIGER* AN ENVIROTYPIC Pb ELEMENT OF AN *IDIOPRIONIODUS* APPARATUS?

The *Idioprioniodus* apparatus was reconstructed early in the history of conodont apparatus reconstruction, before standard element terminology was established. Each author introduced his own notation or terminology to describe the elements within the apparatus. The resulting multitude of systems can lead to confusion. Text-figure 1 shows the equivalency of terminology of the primary schemes used to describe elements in *Idioprioniodus* apparatuses.

Herein, we follow Klapper and Philip (1971) in developing descriptive terminology based upon form taxonomy for conodont elements. If the form genus name describes sufficiently the conodont element, the name is modified by adding the suffix '-an' to the root of the name. For example, the form genus *Geniculatus* becomes geniculatan. For genera, such as *Polygnathus*, which have scores of morphologically distinct species, the genus name alone is insufficiently descriptive. The trivial name of the appropriate species, modified by adding the suffix '-iform' to the root of the name, is used to describe the conodont. For example, the Pa element of the *Polygnathus communis* Branson and Mehl apparatus is communiform.

Hass (1953) named the form genus *Geniculatus* for specimens recovered from the Lower Carboniferous Barnett Formation in Texas and referred originally to the form species *Polygnathus? claviger* by Roundy (1926). Hass described the conodonts as 'geniculate, asymmetric, massive bar-like units which taper from the vertex toward the anterior and posterior extremities.' Using a size gradation of specimens, he interpreted the ontogeny as beginning with small, fragile, bar-like conodonts and developing into massive elements.

Merrill (1980) noted that not all specimens included in the form species *Geniculatus claviger* (Roundy) developed massive bar-like processes (Pl. 1, figs 1, 4, 11–13). Those lacking this development (Pl. 1, figs 2–3), he referred to as 'ponderosa' elements (ponderosiform herein) because of their similarity to form species *Lonchodina? ponderosa* Ellison. Merrill further reported that, although both geniculatan and ponderosiform elements can co-occur, samples lacking the geniculatan elements interfinger with those containing them in the Barnett Formation. Geniculatan elements are more common in the lower and upper parts of the formation, but are relatively uncommon in the middle third. Because of its distribution and unusual platform development. Merrill (1980), Merrill and Grayson (1987) and Merrill *et al.* (1990) suggested that the geniculatan form is an ecophenotype (herein envirotype) of the ponderosiform elements.

Merrill (1980) and Rexroad (1981) proposed that ponderosiform and geniculatan elements were alternative Pb elements of otherwise identical *Idioprioniodus* apparatuses. In one form, Pb elements were geniculatan and in the other ponderosiform. In 1978, Chauffe informally reconstructed apparatuses from Barnett Formation samples (work unpublished). His reconstructions of *Idioprioniodus*-like apparatuses were identical to those suggested by Merrill (1980) and Rexroad (1981). The apparatus consisted of geniculatan or ponderosiform Pb, neoprioniodan M, hibbardellan (= roundyan) Sa, detortiform Sb_1, metalonchodinan Sb_2 and ligonodinan Sc elements (Text-fig. 1). In contrast, Sweet (1988, p. 83, fig. 5.31) described and illustrated the apparatus as consisting of digyrate pectiniform Pa (= our Sb_2 metalonchodinan?), digyrate pectiniform Pb (= our ponderosiform), dolabrate M, bipennate Sb, bipennate Sc and alate Sa elements.

Merrill (1980) retained the Barnett Formation *Idioprioniodus*-like multielement species in open nomenclature. However, in the same publication Namy (1980) applied the name *Idioprioniodus*

This paper	Namy, 1980 Merrill and Grayson 1987	Chauff 1983	Robinson 1981 Sweet 1988	Nicoll and Rexroad 1975	Merrill and Merrill 1974	Baesemann 1973 Higgins 1982	Bitter 1972
Pb element ponderosiform geniculatan	ponderosiform geniculatan	Pb element "lonchodinan"	Pb element angulate (digyrate pectiniform Sweet,1988)	paraclaviger element	ponderosa element	B3b element	none
M element neoprioniodan	conjunctiform	M element neoprionio-dontan	M element dolabrate	conjunctus element	conjunctus element	N element	Ne element
Sa element hibbardellan (roundyan)	subacodiform	Sa element hibbardellan	Sa element alate	subacoda element	subacodus element	B3a element	Tr element
Sb$_1$ element detortiform	(para) clark-iform	Sb$_1$ element detortiform	digyrate	clarki element	clarki element	B1b element	Pl element
Sb$_2$ element metaloncho-dinan	bidentatiform	Sb$_2$ element metaloncho-dina	digyrate (Pa element? digyrate pectiniform Sweet 1988)	bidentata element	bidentatus element	(N2 Higgins, 1982)	none
Sb$_3$ element lexingtonensi-form	none	Sb$_3$ element lonchodinan	bipennate	none	lexington-ensis element	B2 element	none
Sc element ligonodinan	typiform	Sc element ligonodinan	bipennate	typa element	typus element	B1a element	Hi element

TEXT-FIG. 1. Major notation schemes to identify elements in *Idioprioniodus* apparatuses. In Robinson (1983), only Pb and M elements are identified specifically as to shape categories. Symmetry-transition elements are described as ranging from late through digyrate to bipennate. Sweet (1988, fig. 5.31) placed what we interpret to be a metalonchodinan element in the Pa position in the apparatus. We have assigned shape categories to S elements illustrated in Robinson (1983) and Sweet (1988).

paraclaviger (Rexroad) in his plate descriptions to a reconstruction containing both ponderosiform and geniculatan elements. There was no discussion in the text and it is unclear if Namy interpreted both of them as elements of one apparatus or as alternative Pb elements within one apparatus type. Namy's plate and plate description were republished in Merrill and Grayson (1987), although within the text the name *I. paraclaviger* was not used. Merrill *et al.* (1990) again employed open nomenclature for the two forms of *Idioprioniodus* apparatuses.

If the geniculatan and ponderosiform elements are ecotypes, ecophenotypes or envirotypes, their apparatuses are conspecific and only one species name is required. If they represent distinct species or subspecies, a nomenclatural distinction must be made. We believe that applying the five criteria proposed herein will provide an objective evaluation of the relationship between the two phenotypes. Analysis results are listed below.

(1) None of the other five multielement species in the Barnett Formation conodont fauna display consistent modifications, as do the geniculatan elements.

(2) Only geniculatan Pb elements of the *Idioprioniodus* apparatus are modified. Apparatus elements that would have been associated with geniculatan elements can not be distinguished from those associated with ponderosiform elements. The more rapid evolution of Pb elements, compared with the remainder of the apparatus, would be consistent with the model of mosaic evolution for many conodont apparatuses. *Idioprioniodus* may, however, be an exception to this rule, as demonstrated by the more rapid evolution of lexingtonensiform Sb_3 and metalonchodinan (= bidentatiform) Sb_2 elements during the Late Carboniferous.

(3) Modification is the asymmetrical platform development on the Pb element. Platform development on Pa elements is known from the Ordovician through to the Triassic. Although less common on Pb elements, it is not unusual. Platforms developed on form species of *Elictognathus*, *Nothognathella* and others. Merrill (1980), Merrill and Grayson (1987) and Merrill *et al.* (1990) refer to the geniculatan platform as a 'pseudoplatform' or 'bizarre platform surrogate'. We could find nothing that distinguishes the geniculatan platform from platforms developed on some form species of *Nothognathella*. Microstructure of the geniculatan platform displays normal conodont structure.

(4) Distribution of ponderosiform and geniculatan phenotypes suggests their geographical ranges overlapped only at the periphery. Although there is variation in extent of platform development, it is not possible to demonstrate a cline.

(5) The interfingering relationship displayed by the two phenotypes could have been produced if either phenotype distribution was environmentally controlled or the geniculatan form was environmentally induced.

Thompson and Fellows (1970) reported a similar distribution of form species *Gnathodus cuneiformis* Mehl and Thomas from the Osagean Series of the Midcontinent. *G. cuneiformis* appears only at the bottom and top of several sections although other closely related species of *Gnathodus* occur throughout. Thompson and Fellows interpreted the upper *G. cuneiformis* as a homeomorph of the lower form. From conodont multielement species diversity data, Chauff (1983) reinterpreted the occurrence of *G. cuneiformis*, proposing that the distribution was environmentally controlled by water depth or distance from shore. The species was absent from the part of the section representing maximum transgression.

From our analysis, we find little evidence to suggest that the geniculatan element should be considered an ecophenotype or envirotype. We believe the geniculatan element evolved from the ponderosiform element and does not represent an environmentally induced phenotype. Although we concede that the geniculatan element could be an ecotype, this is a moot point considering available data.

The taxonomic level at which apparatuses with geniculatan Pb elements should be recognized is a matter of subjective interpretation. There is no reliable correlation between morphology and reproductive isolation. At one extreme, sibling species are morphologically identical but reproductively distinct, although their ranges may coincide or overlap. At the opposite extreme, envirotypes, ecotypes and ecophenotypes may be morphologically dissimilar, but are conspecific. There is no reliable guideline determining what differentiates conodont form or multielement subspecies, species and genera.

As a form taxon, *Geniculatus claviger* would be considered sufficiently distinct to be the basis of a form genus. In multielement or apparatus taxonomy, differences within the entire apparatus must be considered. Modification of one element is usually recognized to be of lesser taxonomic importance. We feel the degree of genetic separation indicated by the development of the geniculatan element is sufficiently important to recognize a separate species at this time. We follow Chauff (1983) in questioning the assignment to *Idioprioniodus* of multielement species which differ substantially from the type species, *I. cornutus* (Stauffer and Plummer), in element composition. Thus, we recognize two species of questionable *Idioprioniodus* in the Barnett Formation: *I.? healdi* bears the ponderosiform Pb element and *I.? claviger* contains the geniculatan Pb element.
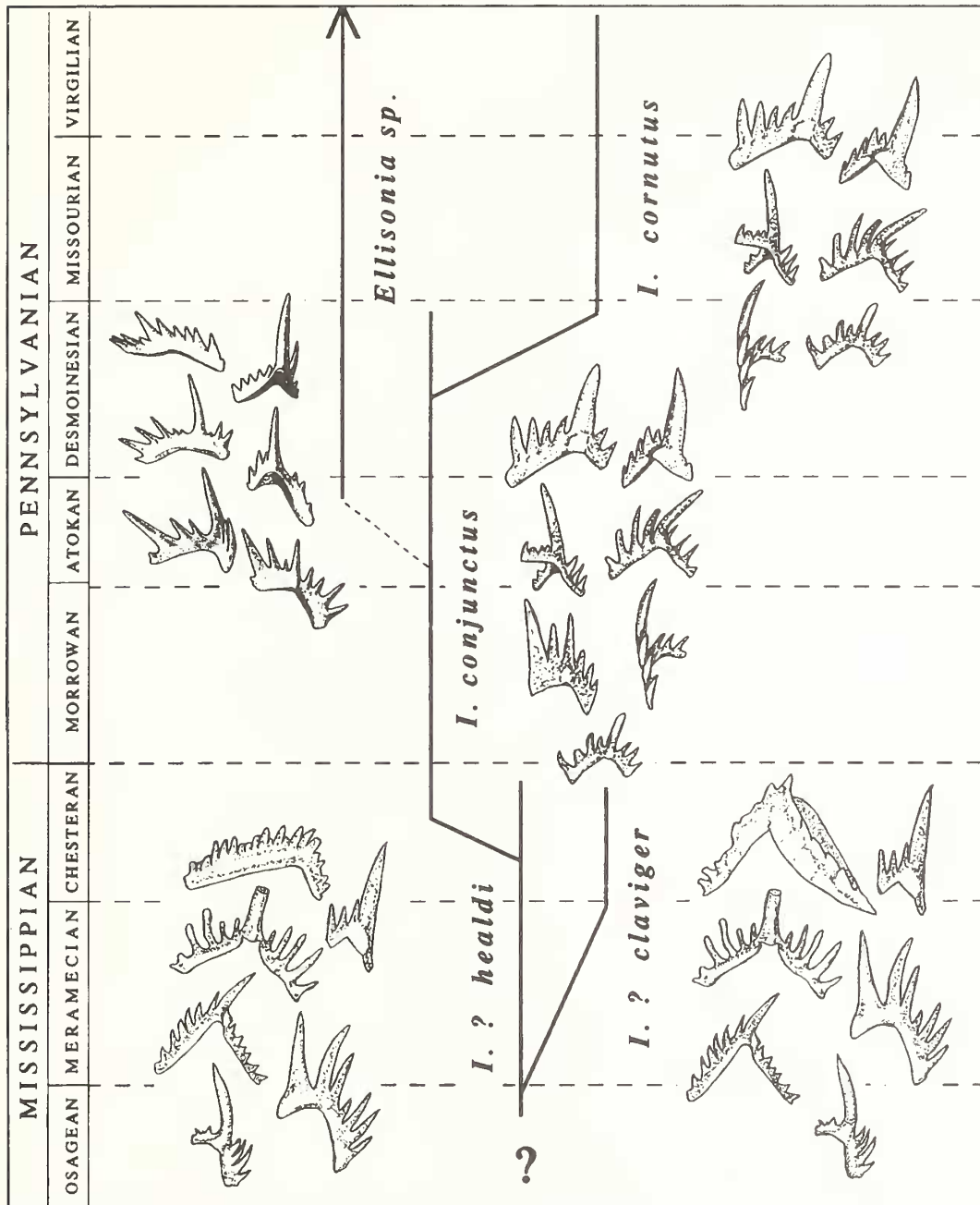
TEXT-FIG. 2. Phylogeny of *Idioprioniodus* spp. Illustration of *Ellisonia* is redrawn from Sweet (1988); all others original.

PHYLOGENY OF MULTIELEMENT *IDIOIPRIONIODUS* SPECIES

The multielement genus *Idioprioniodus*, including species assigned with question, is restricted to the Carboniferous. It ranges from Osagean (Lower Carboniferous) to Virgilian (Upper Carboniferous). The ancestor of the genus is unknown. Elements similar to those in multielement *Idioprioniodus* occur in Upper Devonian and Kinderhookian (basal Carboniferous) faunas. Few apparatuses have been reconstructed from the Kinderhookian, so it is uncertain if the *Idioprioniodus*-like elements are related directly to *Idioprioniodus*. Except for the addition of a Pa element, the Upper Devonian apparatus *Cryptotaxis culmunidirecta* (Scott) not only has an identical element composition to *Idioprioniodus*? *healdi*, but many of the elements are also nearly identical. This is not to imply that *Cryptotaxis* is the ancestor of *Idioprioniodus*, although they are probably related. However unlikely, one can not discount the possibility that similarity in element composition and form may reflect only similarity of habitat and niche, and little about phylogenetic relationships.

    Idioprioniodus? *healdi* is the first known *Idioprioniodus* species in the Midcontinent and occurs in the Upper Osagean (Text-fig. 2). By the Chesteran, *L.*? *claviger* appears as a well developed species. It may have evolved as early as Late Osagean or Meramecian from *I.*? *healdi* by the development of an asymmetrical platform on the Pb element. Nicoll and Rexroad (1975) and Chauff (1983) reported Valmeyeran (= Osagean) ponderosiform (= paraclavigiform) elements with lateral thickenings along the processes. These specimens are large and the thickenings may be 'gerontic features', not the initial stages in the evolution of geniculatan elements. Chesteran *I.*? *claviger* are not known from the Upper Carboniferous.

    Also during the Chesteran, *I.*? *healdi* evolved into *I. conjunctus* (Gunnell) by addition of a lexingtonensiform [lonchodinan Sb_3] element to the apparatus. *I. conjunctus* persisted until near the top of the Desmoinesian, where its apparatus gradually lost the Sb_2 metalonchodinan (= bidentatiform) element and evolved into *I. cornutus* (Stauffer and Plummer), the type species for the genus. For a time, both *I. conjunctus* and *I. cornutus* co-existed but, in the Missourian, no *I. conjunctus* remain (Merrill and Merrill 1974). By the Virgilian, faunas contain few elements belonging to *Idioprioniodus*. The multielement genus is not known from the Permian.

    Sweet (1988) proposed that the multielement genus *Ellisonia*, and possibly *Xaniognathus*, evolved from *Idioprioniodus* during the Atokan (Upper Carboniferous). He listed the major differences between contemporaneous *Idioprioniodus* and *Ellisonia* as longer and more profusely denticulate processes in *Ellisonia*, and larger basal pit and less prominent zone of recessive basal margin in *Idioprioniodus*. In contrast, Bitter and Merrill (1983) suggested that *Ellisonia* possibly evolved from *Magnilaterella*.

    Merrill and Merrill (1974) proposed that multielement *Idioprioniodus* species were dimorphic. Two similar, yet slightly different apparatuses occur in the same faunas. Horowitz and Rexroad (1982) also suggested that a dimorphic pair was present in their study. One dimorph contained form species *Lonchodina furnishi* and the other *L. paraclaviger* as Pb elements. Restudy of Chauff's (1983) Osagean faunas suggests that a dimorphic pair was present. He illustrated two slightly different Pb elements in his plate 3, figures 26, 30 and 32. From our limited collection, we could not identify dimorphs of *I.*? *claviger*.

BLADE POSITION ON *TAPHROGNATHUS VARIANS* Pa ELEMENTS AS AN ENVIRONMENTALLY INDUCED FEATURE

Purnell (1992) rejected the practice of establishing taxa on the basis of blade position relative to platform shape and ornamentation on Pa elements from the *Taphrognathus varians* Branson and Mehl apparatus. He demonstrated that blade position changed during 'ontogeny', as interpreted from a size gradation of specimens, and suggested that it may also have been environmentally induced.

    From blade position, Purnell (1992) recognized 13 categories of Pa element of the *Taphrognathus varians* apparatus. These he grouped into three distinct morphotypes. For the Bogside Limestone

Member at his locality 10, Purnell plotted category occurrence against an arrangement of samples reflecting a gradient of increasing environmental restriction. Morphotype II, approximately equivalent to form species *Cloghergnathus globenskii* Austin, and Morphotype I were shown to be limited to the most restricted environment, whereas Morphology III ranged into normal marine conditions in this section. Purnell observed that the distribution of morphotypes reflected increasing variability of blade position with increasing environmental restriction, but noted that this was possibly a sampling artefact. He proposed that blade position may have been an environmentally controlled character, an envirotype (his ecophenotype).

Purnell also stated that the three morphotypes were not randomly distributed geographically. American faunas are dominated by Morphotype I, Irish faunas by Morphotype II and his Northumberland faunas by Morphotype III. He found that the morphotypes are not geographically mutually exclusive and show considerable overlap in range of variation.

Unlike the form species *Geniculatus claviger*, we have had limited experience with *Taphrognathus varians* as either a form or multielement species. We have no experience with Purnell's British faunas. Thus, our evaluation of the relationship between these phenotypes is largely from information provided in Purnell (1992).

(1) Purnell cites no modified elements in other multielement species in the fauna.

(2) Only Pa elements in the *Taphrognathus varians* apparatus display modification. Other elements in the apparatus appear to have been vicarious among the three morphotypes and 13 categories.

(3) The modification of the Pa element is the location of blade relative to platform and platform ornamentation. For conodonts, platform ornamentation can be variable or constant depending on the species. In some species platform shape in relation to blade can also vary.

(4) Data presented in Purnell's text-figure 8 indicated that all morphotypes of *T. varians* co-occurred within the restricted and fluctuating environment in the Bogside Limestone Member. Morphotypes I and II appear limited to this environment, whereas Morphotype III ranged into normal marine conditions. Purnell demonstrated no gradation of morphologies along the proposed environmental cline.

These data indicate that Purnell's morphotypes had to be genetically distinct, otherwise different morphotypes would not have occurred in the same environment. Two possibilities exist. In the first, blade position was a genetically controlled (broadly canalized) feature. Distribution of the three genetically distinct morphotypes was environmentally controlled, but not environmentally induced. Morphotypes I and II inhabited mainly restricted habitats, whereas Morphotype III inhabited a wide range of environments. The three morphotypes could co-occur only in restricted environments, as they did in the Bogside Limestone Member.

The second possibility is that blade position was a 'developmentally flexible' feature. Specific morphotypes developed in response to environmental conditions and the genotype of individual organisms. Under normal marine conditions all individuals matured into the range of forms classified as Morphotype III. However, in a restricted environment, some genetic variants (sub-populations) matured into either Morphotypes I or II (Purnell's ecophenotype, our envirotype). The remainder of the population developed as Morphotype III even in restricted environments because they lacked the genetic potential to be altered by the environmental stimuli.

The geographical restriction of Morphotype III to primarily Northumberland faunas argues against Morphotypes I and II being envirotypes induced by a restricted environment. As indicated in the Bogside Limestone Member, Morphotype III occurred in restricted and open marine environments. As such, it should have occurred in, and dominated, all geographical areas containing Morphotype I and II. The near absence of Morphotype III from American and Irish faunas suggests that other factors controlled this morphotype's distribution. It also strongly suggests that Morphotypes I and II were genetically distinct sub-populations dominating large geographical areas encompassing a variety of environments.

(5) All of the morphotypes appear to be long-ranging and not restricted to single time horizons or specific lithology.

We feel the data do not support the assertion that blade position on Pa elements in the *T. varians* apparatus is an environmentally induced character. Sufficient evidence exists to suggest that genetic differentiation among the three morphotypes accounted for their differences in morphology and distribution. They may be considered to represent distinct populations, subspecies or perhaps ecotypes.

The same morphotype distribution of Pa elements of *T. varians* could be explained by low gene flow among genetically distinct populations. Temporary isolation of an initially homogeneous population would allow mutations, such as those controlling blade position, to accumulate and eventually dominate a population and geographical area. When reunited, gene flow between populations may have been limited and diluted by the large existing gene-pool of the indigenous population. If blade position offered no survival advantage, no morphotype would necessarily have become dominant outside the area where it developed. Over time, dispersal of genes introduced into a gene-pool would account for the overlap in range of variation shown within the geographical areas.

CONCLUSIONS

There is no standard phenotype for an organism. All phenotypes represent the interaction of environment and genotype. The same genotype exposed to different environments may produce different phenotypes. Some phenotypes are stable and persist for as long as the environment exists. These phenotypes must therefore be considered potentially inheritable. As such, they are not ecophenotypes. The name ecophenotype should be restricted to phenotypic modifications resulting from disease, injury, physical restrictions to growth or modifications that develop through use.

Envirotypes are persistent, consistent, environmentally induced, potentially inheritable phenotypes that have not been selected genetically for a given environment. Different conspecific envirotypes bred in the same environment should produce an indistinguishable range of phenotypes.

By considering the number of taxa displaying modifications, number of modified element types within an apparatus, uniqueness of modification, occurrence of modified and unmodified forms and stratigraphical range of modified forms, it is possible to evaluate objectively whether modifications in conodonts represent evolution or environmentally induced changes.

Development of geniculatan from ponderosiform Pb elements represents evolution. The multielement species *I.? claviger* contains geniculatan Pb elements and *I.? healdi* has ponderosiform Pb elements. Other elements in the two apparatuses are vicarious. Both species are questionably placed in the genus *Idioprioniodus* because their element composition differs substantially from that of the type species, *I. cornutus*.

The *Idioprioniodus* lineage begins with *I.? healdi. I.? claviger* evolved from *I.? healdi* as early as late Osagean or early Meramecian by the development of the geniculatan Pb element. *I.? claviger* is not known from the Upper Carboniferous. *I.? healdi* evolved into *I. conjunctus* during the Chesteran by adding a lonchodinan (lexingtonensiform) Sb_3 element to the apparatus. By the Missourian, *I. conjunctus* evolved into *I. cornutus* by the loss of the metalonchodinan Sb_2 element. The multielement genus *Idioprioniodus* is not known from the Permian. *Idioprioniodus* spp. may have occurred as dimorphic pairs.

Distribution of morphotypes of the Pa elements of *Taphrognathus varians* suggests that blade position relative to platform and platform ornamentation was genetically controlled, not environmentally induced.

SYSTEMATIC PALAEONTOLOGY

Although reconstructed and discussed by several workers, none has provided a synonymy for elements of the *Idioprioniodus*? apparatuses from the Barnett and related formations. We employed a conservative approach in synonymizing form species as apparatus elements and restricted our

consideration to Osagean and Chesteran faunas. Only references readily available to us containing adequate illustrations and/or descriptions that permitted identification with some confidence have been included. Synonymies are, therefore, not intended to be comprehensive.

Apparatus element notation follows Sweet and Schönlaub (1975), but has been modified where necessary. Element descriptive terminology is developed along the guidelines established in Klapper and Philip (1971). Specimens are reposited at The Department of Earth and Atmospheric Sciences, Saint Louis University (SLU), St Louis, Missouri 63103, USA.

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Phylum CONODONTA Eichenberg, 1930
Class CONODONTA Eichenberg, 1930
Order CONODONTOPHORIDA Eichenberg, 1930
Superfamily HIBBARDELLACEA Müller, 1956
Family HIBBARDELLIDAE Müller, 1956

Genus IDIOPRIONIODUS Gunnell, 1933

</div>

Form genera.

1933   *Idioprioniodus* Gunnell, p. 265.
1953   *Geniculatus* Hass, p. 77.
1953   *Roundya* Hass, p. 88.
1956   *Neoprioniodus* Rhodes and Müller, p. 698.

Multielement genera.

1952   *Duboisella* Rhodes, p. 895.
1972   *Neoprioniodus* Bitter, p. 68.
1973   *Idioprioniodus* Baesemann, p. 703.
1974   *Idioprioniodus* Merrill and Merrill, p. 119.
1975   *Idioprioniodus* Nicoll and Rexroad, p. 20.
1981   *Idioprioniodus* Robinson, p. 149.
1983   *Idioprioniodus* Chauff, p. 418.

Type species. Idioprioniodus cornutus (Stauffer and Plummer, 1932), by subsequent designation (Merrill *et al.* 1987).

Diagnosis. Elements Pb = ponderosiform or geniculatan, M = neoprioniodan, Sa = hibbardellan (roundyan), Sb_1 = detortiform, Sb_2 = metalonchodinan and/or Sb_3 = lexingtonensiform, Sc = ligonodinan.

Remarks. Determining the variability allowed under the definition of a genus is a problem that multielement taxonomy has not resolved. Each genus must be treated individually. Guidelines used for one genus may not be applicable to another. For example, multielement species of *Bactrognathus* differ primarily in Pa element morphology. Apparatus element composition remained unchanged. In contrast, variation in apparatus element composition has defined species of *Idioprioniodus* (Merrill and Merrill 1974). The difference between *I. conjunctus* and the type species *I. cornutus*, the senior synonym of *I. typus* (Merrill *et al.*, 1987), is absence of the metalonchodinan (bidentatiform) Sb_2 element in *I. cornutus*. Otherwise, the apparatuses are nearly identical.

As earlier multielement species related to *Idioprioniodus* are reconstructed, differences from the type species increase. For example, *I.? healdi* contains no lexingtonensiform Sb_3 element, but has metalonchodinan (= bidentatiform) Sb_2 elements. *I.? claviger* is even more distinct. It has the same element composition as *I.? healdi*, but its Pb element is geniculatan, not ponderosiform. The point at which a species is considered sufficiently distinct from the type species such that it becomes necessary to create a new genus depends upon a palaeontologist's bias.

Some may argue that *I.? healdi* and *I.? claviger* are already sufficiently different from *I. cornutus* that they should be placed in a separate genus. Creating a new genus could obscure the close evolutionary relationship between these species. Yet, placing them in the same genus implies that these species are very similar to the type species.

We have chosen to follow Chauff (1983) and question the assignment to *Idioprioniodus* of multielement species which differ substantially from the type species. Thus, we retain *I.? healdi* and *I.? claviger* within *Idioprioniodus*, but question the assignment. This will allow us to indicate the close relationship with other species of *Idioprioniodus* and also imply that major differences exist with the type species.

Sweet (1988, fig. 5.31) illustrated an *Idioprioniodus* apparatus in which he placed what appears to be the metalonchodinan element in the Pa position. We find this to be inconsistent with reconstructions of morphologically similar multielement genera. For example, the apparatuses of *Bactrognathus* and *Cryptotaxis* bear metalonchodinan elements, as well as Pa elements. In both of these apparatuses, the metalonchodinan element is placed within the symmetry transition series. The distinctive shape of the metalonchodinan element evolved probably to perform a specific task within the apparatus. Thus, we feel it is unlikely that the same element morphology occupies different positions in similar apparatuses.

Idioprioniodus can be distinguished from *Cryptotaxis* and *Bactrognathus* because both of these multielement genera possess Pa elements. See Chauff (1983, p. 419) for additional information regarding differences between these genera.

Voges (1959) named the form species *Geniculatus glottoides* from the 'Dunne Kalkbank an der Grenze Liegende Alaunschiefer/Horizont vorwiegender Lydite'. This form species is unlike *Geniculatus claviger* because its wide platform is concave-up and denticles on the anterior process are small, possibly fused into a low ridge. Voges (1959) did not illustrate any ramiform elements from the fauna containing *Geniculatus glottoides*. Thus, it is not possible to determine if this form species was associated with elements similar to those assigned to the *I.? claviger* apparatus.

Range. Osagean through Upper Carboniferous.

Idioprioniodus? claviger (Roundy, 1926)

Plate 1, figures 1, 4, 11, 13–14

Pa element.

1926	*Polygnathus claviger* Roundy, p. 14, pl. 4, figs 1a–c, 2a–b.	
1941	*Bactrognathus inornata* Branson and Mehl, p. 100, pl. 19, figs 14–15.	
1953	*Geniculatus claviger* Hass, p. 77, pl. 15, figs 10, 12, 14–16, 18–19 [*non* figs 11, 13, 17 = *L.? healdi*; figs 10, 12 cops Roundy, 1926].	
1956	*Geniculatus claviger* Elias, p. 121, pl. 4, figs B8–B13, B19–B21 [*non* figs B14–18 = *I.? healdi*; cops Roundy (1926) and Hass (1953)].	
?1957	*Geniculatus claviger* Bischoff, p. 21, pl. 1, figs 2–4 [figs 1, 5–6 may be *I.? healdi*].	
?1969	*Geniculatus claviger* Druce, p. 60, pl. 8, figs 8–10.	
1978	*Geniculatus inornatus* Chauff and Klapper, pl. 2, figs 1–2 [cops Branson and Mehl (1941)].	

Multielement.

1980	*Idioprioniodus paracliviger* Namy, pl. 5, figs 32–36, 39–42 [*non* figs 37–38 = *I.? healdi*].	
1987	*Idioprioniodus paraclaviger* Merrill and Grayson, p. 72, pl. 7, figs 32–36, 39–42 [*non* figs 37–38 = *I.? healdi*; cops Namy, 1980].	

Diagnosis. Elements Pb = geniculatan, M = neoprioniodontan, Sa = hibbardellan (roundyan), Sb_1 = detortiform, Sb_2 = metalonchodinan, Sc = ligonodinan. Pb elements are arched, have an outcurved anterior process and long, curved posterior process and develop asymmetrical ledges or

platforms along both processes. Denticles are discrete to partially fused. Other elements of apparatus are discussed under Vicarious Elements of *I.? claviger* and *I.? healdi.*

Remarks. From the description and holotype illustration of *Polygnathus? claviger*, it is obvious that Roundy (1926) applied the name to a geniculatan element. Thus, the correct name for the apparatus containing geniculatan Pb elements is *Idioprioniodus? claviger* (Roundy).

The multielement species *I.? claviger* is known from the Barnett Formation in Texas and the Caney Shale and Sycamore Formation *sensu* Branson and Mehl (1941) (i.e. the post-Weldon Shale of Ormiston and Lane 1976) of Oklahoma. Possible Pa elements have been identified in Germany (Voges 1959; Bischoff 1957) and Australia (Druce 1969). The specimens illustrated by Bischoff (1957) and Druce (1969) as *Geniculatus claviger* appear to be within the range of variation recognized for the form species. Until the apparatus composition for these elements is demonstrated, we prefer to question their assignment to *I.? claviger.* *I.? claviger* differs from other species of *Idioprioniodus* by the development of a long posterior process and an asymmetrical platform on its Pb element. Some Pb elements resemble the Sb_1 detortiform element, but with a platform and less pronounced cusp.

Range. Chesteran (Lower Carboniferous).

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Idioprioniodus? healdi (Roundy, 1926)

Plate 1, figures 2–3

</div>

Pa elements.

  1926 *Prioniodus healdi* Roundy, p. 10, pl. 4, fig. 5a–b.
  1926 *Prioniodus* sp. D Roundy, p. 11, pl. 4, fig. 13a–b [*non* fig. 12 = M element].
 ?1940 *Metalonchodina?* sp. Branson and Mehl, p. 172, pl. 5, fig. 15 [possibly an M element].
 ?1940 *Euprioniuodina?* sp. Branson and Mehl, p. 171, pl 5, figs 17–18.
  1953 *Geniculatus claviger* Hass, pl. 15, figs 11, 13, ?17 [*non* figs 10, 12, 14–16, 18–19 = *I.? claviger*; figs 11, 17 cops Roundy (1926)].
  1956 *Geniculatus claviger* Elias, pl. 4, figs 14–18 [*non* figs 8–13, 19–21 = *I.? claviger*; cops Roundy (1926) and Hass (1953)].
  1956 *Geniculatus longiden* Elias, p. 121, pl. 4, figs D27–D29.
 ?1957 *Geniculatus claviger* Bischoff, pl. 1, figs 1, 5–6 [*non* figs 2–4 = *I.? claviger?*].

Multielement.

  1980 *Idioprioniodus paraclaviger* Namy, pl. 5, figs 32–38 [*non* figs 32–36, 39–40 = *I.? claviger*].
 non 1981 *Idioprioniodus* sp. aff. *I. healdi* Rexroad, p. 11, figs 6–8. [most probably *I. conjunctus*].
 non 1982 *Idioprioniodus healdi* Horowitz and Rexroad, 1982, p. 965, text-fig. 7 (line drawing). [= *I. conjunctus*]
  1983 *Idioprioniodus conleyharpi* Chauff, p. 418, pl. 3, figs 22–23, 25–34.
  1987 *Idioprioniodus paraclaviger* Merrill and Grayson, p. 72, pl. 7, figs 32–38 [*non* figs 32–36, 39–40 = *I.? claviger*; cops Namy 1980].

Diagnosis. Elements Pb = ponderosiform, M = neoprioniodontan, Sa = hibbardellan (roundyan), Sb_1 = detortiform, Sb_2 = metalonchidinan, Sc = ligonodinan. Pb elements are arched and have an outcurved anterior process. Denticles are discrete to partially fused at base. Other elements of apparatus are discussed under Vicarious Elements of *I.? claviger* and *I.? healdi.*

Remarks. Namy (1980) applied the name *Idioprioniodus paraclaviger* (Rexroad) to the Barnett Formation apparatus, presumably because of its similarity in element composition to a reconstruction called *I. paraclaviger* by Nicoll and Rexroad (1975) from the Sanders Group. The type specimen of *I. paraclaviger* (holotype of form species *Lonchodina paraclaviger*) was from the Chesterian Glen Dean Limestone, not the Valmeyeran (= Osagean) Sanders Group. Nicoll and

Rexroad suggested that the name *I. paraclaviger* might prove to be inappropriate for the Valmeyeran species.

Norby (1976) restudied the conodont fauna of the Glen Dean Limestone and demonstrated that lexingtonensiform (lonchodinan Sb_3) elements were probably part of the apparatus containing the type specimen of *Lonchodina paraclaviger*. Although it is possible that apparatuses with and without the lexingtonensiform element co-existed in the Glen Dean Limestone, this cannot be determined from available data. No lexingtonensiform elements have been reported from the Sanders Group or Barnett Formation. Therefore, the *Idioprioniodus* apparatus species bearing ponderosiform Pb elements in these strata cannot be the same species as in the Glen Dean Limestone. The name *I. paraclaviger* is inappropriate and another name is needed. Because the apparatus Norby reconstructed is identical in element composition to *I. conjunctus*, the form species name *I. paraclaviger* is a junior synonym of *I. conjunctus*.

Chauff (1983) reconstructed an *Idioprioniodus*-like apparatus from the Osagean of the Midcontinent and proposed the name *Idioprioniodus*? *conleyharpi*. It has the same element composition as the apparatus in the Sanders Group and the apparatus containing ponderosiform Pb elements in the Barnett Formation.

Roundy (1926) named *Prioniodus healdi* for a small conodont fragment consisting of a sharp-edged, compressed cusp and one denticle from each process. Holotype illustrations, especially of the lower side, show a marked offset of the processes at the cusp. Hass (1953) placed this form species into synonomy with *Geniculatus claviger* and designated the *P. healdi* holotype as a hypotype for *G. claviger*. Although we have not seen the *P. healdi* type specimen, we believe it represents a ponderosiform element, not a small (immature) geniculatan element. The name *Prioniodus healdi* is senior to *I*.? *conleyharpi* and the valid name for the Osagean and Barnett Formation multielement species containing ponderosiform Pb elements is *Idioprioniodus*? *healdi*.

Rexroad (1981) and Horowitz and Rexroad (1982) applied the name *Idioprioniodus healdi* (Roundy) to conodont apparatuses from the Vienna Limestone Member of the Branchville Formation and from the Glen Dean, Beech Creek and Reelsville limestones (all Chesteran). Because geniculatan Pb elements have not been recovered in the Midcontinent, identification of Chesteran *Idioprioniodus* apparatus species depends primarily upon the presence or absence of a lexingtonensiform Sb_3 element. Without the lexingtonensiform element the apparatus is *I*.? *healdi*; with it the apparatus is *I. conjunctus*. *I*. sp. aff. *I. healdi* (Roundy in Rexroad 1981) must be considered a dubious designation. Identification was based upon a few fragmentary M, Sb_1 (detortiform) and Sc (ligonodinan) elements. The Vienna Limestone Member is higher in the section than the Glen Dean Limestone, from which only *I. conjunctus* is known. Thus, it is more likely that the elements in the Vienna Limestone belong to *I. conjunctus*, than *I*.? *healdi*.

I. healdi, as reported in Horowitz and Rexroad (1982), is based again on a small number of specimens. From line illustrations in their text-figure 7, it is clear that Horowitz and Rexroad considered the apparatus to contain lexingtonensiform Sb_3 elements. This clearly would be *I. conjunctus*, not *I*.? *healdi* as defined herein.

EXPLANATION OF PLATE 1

Figs 1, 4, 11, 13–14. Pa elements of *Idioprioniodus*? *claviger* (Roundy). 1, 4, SLU 507; upper and lower views. 11, 14, SLU 508; upper and lower views. 13, SLU 509; outer lateral view.

Figs 2–3. Pa elements of *I*.? *healdi* (Roundy). 2, SLU 510; outer lateral view. 3, SLU 511; inner lateral view.

Figs 5–10, 12. Vicarious elements of *I*.? *healdi* and *I*.? *claviger*. 5, SLU 512; inner lateral view of neoprioniodan M element. 6, SLU 513; lateral view of hibbardellan (roundyan) Sa element. 7, SLU 514; inner lateral view of detortiform Sb_1 element. 8–9, SLU 515 and 516; inner lateral view of metalonchondinan Sb_2 elements. 10, SLU 517; inner lateral view of ligonodinan Sc element. 12, SLU 518; posterior view of hibbardellan (roundyan) Sa element.

All specimens from Zesch Ranch; Barnett Formation (Chesteran, Lower Carboniferous). All × 44.

PLATE 1

CHAUFFE and NICHOLS, *Idioprioniodus*?

Osagean *Idioprioniodus*? *healdi* is discussed in Chauff (1983) under the junior synonym *I.*? *conleyharpi*. Chesteran *I.*? *healdi* appears to be identical to the Osagean form. This species differs from other *Idioprioniodus* species because it has a ponderosiform Pb element and a metalonchodinan Sb$_2$ element, but no lexingtonensiform Sb element.

Range. Osagean into Chesteran (Lower Carboniferous).

Vicarious Elements of *Idioprioniodus*? *claviger* and *I.*? *healdi* from the Chesteran

Plate 1, figures 5–10, 12

M elements.

?1926	*Prioniodus* sp. B Roundy, p. 11, pl. 4, fig. 9.	
1926	*Prioniodus* sp. D Roundy, p. 11, pl. 4, fig. 12 [*non* fig. 13a–b = Pa element of *I.*? *healdi*].	
?1953	*Prioniodus ligo* Hass, p. 87. pl. 16, figs 1–3.	
1953	*Prioniodus inclinatus* Hass, p. 87, pl. 16, figs 10–14 [fig. 12, cop. Roundy (1926)].	
1956	*Prioniodus*? *inclinatus* Elias, p. 112, pl. 4, figs 4–7 [cops Roundy (1926) and Hass (1953)].	

Sa Elements.

1953	*Roundya barnettana* Hass, p. 88, pl. 16, figs 8–9.
1956	*Roundya barnettana* Elias, p. 121, pl. 4, figs 22–23 [cops Hass (1953)].
1956	*Roundya* sp. A Elias, p. 121, pl. 4, fig. 26.

Sb$_1$ Element.

?1926	*Prioniodus* sp. C Roundy, p. 11, pl. 4, fig. 11 [may be Sc element].
1953	*Lonchodina paraclarki* Hass, p. 83, pl. 16, figs 15–16.
1956	*Lonchodina paraclarki* Elias, p. 122, pl. 5, figs 6–7 [cops Hass (1953)].

Sb$_2$ Element.

1953	*Metalonchodina* sp. A Hass, p. 85, pl. 16, figs 17–18.
1956	*Metalonchodina* sp. A Elias, p. 126, pl. 5, figs 8–9 [cops Hass (1953)].
1956	*Lonchodina regularis* Elias, p. 122, pl. 5, fig. 20 [figs 19, 21–22 indeterminate].

Sc Element.

?1926	*Prioniodus* sp. C Roundy, p. 11, pl. 4, fig. 11 [may be Sb$_1$ element].
1953	*Ligonodina roundyi* Hass, p. 82, pl. 15, figs 7–9, ?5–6 [figs 5, 6 cops Roundy (1926)].
1956	*Ligonodina roundyi* Elias, p. 126, pl. 5, figs 10–14 [cops Hass (1953)].

Remarks. M elements have high, compressed cusps and smaller, discrete to fused denticles on the posterior process. S elements possess discrete, compressed, high, slender, posteriorly reclined denticles. Cusps are similarly shaped but larger and may be marked by lateral ridges. Denticles on the posterior process of the Sa and Sc elements are variable.

Names of other ramiform species proposed by Hass (1953), such as *Ligonodina roundyi*, *Roundya barnettana*, *Prioniodus inclinatus* and *Lonchodina paraclarki*, all of which are part of either the *I.*? *claviger* or *I.*? *healdi* apparatus, must be considered *nomina dubia*. These elements are vicarious, occurring in apparatuses with geniculatan or ponderosiform Pb elements. It is impossible to determine to which apparatus species the holotypes of these form species belong.

Bischoff (1957) illustrated several elements, including several Pb elements, which may be part of an *Idioprioniodus* apparatus. From data presented in his paper, we could not determine if these elements were associated with the Pb element in an apparatus. Thus, we have not included these elements in the synonymy for vicarious elements.

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KARL M. CHAUFFE

Geology Section
Department of Earth and Atmospheric Sciences
Saint Louis University
3507 Laclede Ave
St Louis, Missouri 63103, USA

PATRICIA A. NICHOLS

Brotcke Engineering Co. Inc.
Geotechnical Drilling Services
750 Merus Ct, Fenton, Missouri 63026, USA